Modelling the control of interceptive actions

Beek, P.J.; Dessing, J.C.; Peper, C.E.; Bullock, D.

published in
Philosophical Transactions of the Royal Society B. Biological Sciences
2003

DOI (link to publisher)
10.1098/rstb.2003.1343

document version
Publisher's PDF, also known as Version of record

THE ROYAL SOCIETY

Published online 6 August 2003

Modelling the control of interceptive actions

P. J. Beek[1*], J. C. Dessing[1], C. E. Peper[1] and D. Bullock[2]

[1]*Institute for Fundamental and Clinical Human Movement Sciences and Faculty of Human Movement Sciences, Vrije Universiteit, Van der Boechorststraat 9, 1081 BT, Amsterdam, The Netherlands*

[2]*Department of Cognitive and Neural Systems, Boston University, 677 Beacon Street, Boston, MA 02215, USA*

In recent years, several phenomenological dynamical models have been formulated that describe how perceptual variables are incorporated in the control of motor variables. We call these short-route models as they do not address how perception–action patterns might be constrained by the dynamical properties of the sensory, neural and musculoskeletal subsystems of the human action system. As an alternative, we advocate a long-route modelling approach in which the dynamics of these subsystems are explicitly addressed and integrated to reproduce interceptive actions. The approach is exemplified through a discussion of a recently developed model for interceptive actions consisting of a neural network architecture for the online generation of motor outflow commands, based on time-to-contact information and information about the relative positions and velocities of hand and ball. This network is shown to be consistent with both behavioural and neurophysiological data. Finally, some problems are discussed with regard to the question of how the motor outflow commands (i.e. the intended movement) might be modulated in view of the musculoskeletal dynamics.

Keywords: catching; hand movement; timing; neural control

1. INTRODUCTION

Since the introduction of skill-oriented (e.g. Whiting 1969) and perception-based (e.g. Turvey 1977) accounts of action in the area of motor control, interceptive actions like catching and hitting have become a focal point of interest in the study of perception–action coupling (e.g. McLeod 1987; Bootsma & Van Wieringen 1990; Michaels & Oudejans 1992; Peper *et al.* 1994; Smeets & Brenner 1995). This is both understandable and appropriate: interceptive actions are 'real-life' instances of perception–action coupling that highlight the human capacity to operate effectively on dynamic events in the environment. The properties of such events (e.g. an approaching flyball) constrain the performance of interceptive tasks both spatially and temporally: the path followed by the end-effector (e.g. a hand or hand-held implement) must intersect that of the approaching object and the end-effector must be at the intersection point at the same time as the object. Human actors can meet such spatio-temporal constraints with a high degree of accuracy: expert cricket-players bat balls with a spatial accuracy in the order of 0.05 m (McLeod 1987), while expert table-tennis players (Bootsma & Van Wieringen 1990) and baseball players (Regan 1997) have been reported to hit balls with a temporal accuracy in the order of 5 ms. These remarkable feats make one wonder: how are the spatio-temporal constraints on interceptive actions accommodated, that is, how are interceptive actions performed?

Rather diverse strategies have been proposed for the control of interceptive actions. One important distinction is that between predictive and prospective control strategies. Predictive strategies involve vision-based predictions of the time and place of interception. The most extreme predictive strategy is the triggering of a pre-programmed hand movement on the basis of some form of critical predictive (temporal) information (e.g. Tyldesley & Whiting 1975). Besides triggering, however, predictive information may also be used to modulate movement after initiation, which may occur in either a time-discrete or a time-continuous fashion (e.g. Lee *et al.* 1983). Prospective strategies are based not on predictive information but on information specifying the currently required movement adjustments that will ultimately culminate in a successful interception. Thus, the actor establishes a particular dynamic relationship with the environment, which leads to success if it prevails (e.g. Chapman 1968; Peper *et al.* 1994).

Predictive strategies have typically been proposed for rapid interceptive actions such as batting a baseball (Hubbard & Seng 1954), smashing in table tennis (Tyldesley & Whiting 1975) and hitting a simulated 'spider' on a computer screen (Smeets & Brenner 1995). If the action is fast, little time is available for online movement adjustment. Furthermore, predictive control constitutes an expedient means to deal with neural, neuromuscular and electromechanical delays. However, a disadvantage of any predictive strategy is that its success depends on the accuracy of the prediction used (which, in general, will be inversely related to the time-span over which the prediction is made). Viewed in this light, it is not surprising that even for fast interceptive actions little or no evidence has been found for mere triggering, whereas several studies

* Author for correspondence (p_j_beek@fbw.vu.nl).

One contribution of 20 to a Theme Issue 'Modelling in biomechanics'.

DOI 10.1098/rstb.2003.1343

have shown that rapid interceptive movements are continuously influenced by visual information about the target (Pélisson *et al.* 1986; Smeets & Brenner 1995).

If even fast interceptive actions are continuously influenced by visual information, then surely slower interceptive actions like catching are. However, it is still an open question whether continuous control strategies used in catching are more appropriately understood as predictive or as prospective. It could be argued that some form of prediction must be used because humans are still able to catch balls when visual information about the ball's flight is only available during a limited time (e.g. Sharp & Whiting 1974; cf. Brouwer *et al.* 2002). However, in catching experiments a remarkable phenomenon has been observed that is difficult to reconcile with the notion of prediction: if the hand is initially positioned at the interception point which the ball approaches under a certain angle, then, at least on some occasions, the hand first moves away from the interception point before reversing direction and returning to it (Montagne *et al.* 1999). Accounting for such 'movement reversals' in terms of prediction requires assuming that the prediction used during the early phase of the action is incorrect and is subsequently improved as the action evolves and more information becomes available.

This brief characterization of the state of affairs in the study of interceptive actions illustrates that many basic issues remain to be resolved, probably owing to the inherent complexity of the problem. The development of a satisfactory account of the control of interceptive actions requires accurate and reliable knowledge not only about the perceptual variables on which control is based but also about the manner in which these perceptual variables support the control of movement. Besides the fact that multiple perceptual variables appear to be used at any one time, probably with context-dependent variations in their precise configurations and relative weightings, these requirements are difficult to accommodate simultaneously because the identification of the type of control depends on the postulated perceptual variables, while the identification of the perceptual variables depends on the postulated control. We will argue that, to break away from this potential deadlock, it is necessary to develop dynamical models for the control of interceptive actions in which as many relevant findings and facts are integrated as possible. Specifically, these findings and facts should not be restricted to the behavioural level, but should also pertain to relevant neuroanatomical, neurophysiological and biomechanical properties of the human action system.

In developing this argument, we distinguish two classes of dynamical models for the control of interceptive actions, called short-route and long-route models (see figure 1). Short-route models formally describe how perceptual and motor variables are coupled onto each other dynamically, thus constituting particular perception–movement dynamics in the form of a dynamical control law (cf. Warren 1988; Schöner 1994). Such phenomenological models provide a short route into the study of interceptive actions in that they do not address how the dynamical properties of interceptive behaviours are instantiated by the human action system. This is the objective of long-route models, which consist of dynamical formulations of the relevant subsystems (i.e. sensory, neural, biomechanical) and their interactions. Until now, the long route has not been fully pursued in the modelling of interceptive actions. Although models of the neural (Dessing *et al.* 2002) and the musculoskeletal system (Van Soest & Beek 1996) have been proposed that address aspects of the control of interceptive actions, a full dynamical neuro-musculoskeletal model has not yet been formulated.

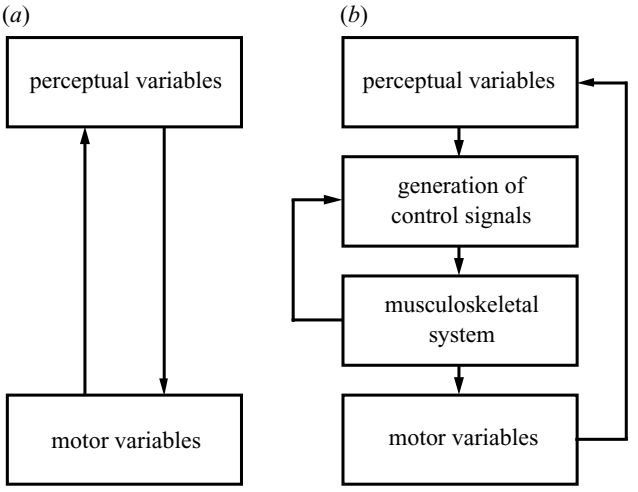

Figure 1. (*a*) 'Short-route' models address the coupling between perceptual variables and motor variables at a behavioural level through dynamical equations of motion. (*b*) 'Long-route' models specifically address how the information carried by perceptual variables is dynamically transformed into appropriate control signals for the musculoskeletal system.

To build our case for the long-route approach, we briefly summarize the pertinent literature on the informational basis of interceptive actions to sketch the current state of affairs in this area. Such a summary is relevant because the identification of adequate perceptual variables is a prerequisite for the construction of both short- and long-route dynamical models. Subsequently, we critically evaluate three short-route models that are currently being pursued in the study of interceptive actions. These steps pave the way for a characterization of the more elaborate (longer) modelling approach and the hurdles to be overcome therein.

2. INFORMATIONAL BASIS OF INTERCEPTIVE ACTIONS

The vast majority of research on interceptive actions has been (and still is) directed at identification of the perceptual variables that play a role in the guidance of such actions. In general, answering this question requires manipulations of the properties of both the to-be-intercepted object (e.g. its size and approach kinematics) and of the visual system (e.g. monocular versus binocular vision, vergence and disparity). Typically, movement kinematics are analysed in relation to the experimental manipulations: if a property of the movement correlates with the manipulations, then the manipulated perceptual variable may be used in the control of action.

However straightforward this approach may sound, it is confronted with several methodological problems. One

persistent problem is that the existence of a correlation as such does not necessarily imply that the perceptual variable of interest was indeed implicated in the control of action. It may have been that another perceptual variable was used, which just happened to be strongly correlated with the variable of interest. Another, but related, problem is that visual manipulations seldom fail to yield statistically significant effects, which leads to the little productive (albeit not necessarily false) conclusion that humans use a large variety of perceptual variables in interceptive actions.

Given these problems, it is impossible to make very definite statements about the perceptual variables that are used in the control of interceptive actions. To summarize the current status of this field of research, it is useful to categorize the pertinent studies into those focusing on 'lower-order variables', motivated from psychophysics and information processing theory, and those focusing on 'higher-order variables', motivated from ecological psychology. Customarily, lower-order variables take the form of either 'standard' kinematical variables (e.g. position, velocity, acceleration and direction of travel) or 'standard' optical and visual variables (e.g. image size, optical angle, vergence, disparity and changes therein). Higher-order variables, by contrast, are ensemble variables composed of lower-order variables. They may be picked up 'directly' from ambient energy patterns (e.g. the optic array), without having to be explicitly calculated from their lower-order constituents (e.g. Runeson 1977). 'Ecological' higher-order variables specify properties of the environment relevant to action, such as TC and place-of-contact.

As regards the use of lower-order variables in interceptive actions, it is evident that some form of information about target location is used (Smeets & Brenner 1995; Brouwer *et al.* 2002). It is also well documented that target velocity has a robust effect on the velocity of the interceptive movement in that one moves consistently quicker to fast targets than to slow ones, the so-called velocity coupling effect (Bootsma & Van Wieringen 1990; Savelsbergh *et al.* 1992; Smeets & Brenner 1995; Carnahan & McFadyen 1996). It appears that position and velocity information play different roles in the control of hitting (Smeets & Brenner 1995), although it is unclear to what extent target velocity affects the actual hand path (in the sense of directional changes; cf. Smeets & Brenner (1995); Brouwer *et al.* (2002), but see also de Lussanet *et al.* (2002*b*)). Even more inconclusive is the evidence with regard to the use of information about target acceleration. Whereas Rosenbaum (1975) reported clear evidence for the use of acceleration in judging when targets moving in a frontal plane reached a certain point, Port *et al.* (1997), who had their subjects actually intercept targets in this plane, found no evidence for the use of acceleration information. All in all, it may be tentatively concluded that humans are most sensitive to position-related information, which they undoubtedly use in interceptive actions, possibly less sensitive to velocity-related information and even less sensitive, if at all, to acceleration-related information.

As regards the use of higher-order variables, it is useful to make a distinction between temporal (TC-related) and spatial (place-of-contact-related) higher-order variables. The former class of variables has been studied more extensively. Since the pioneering work of Lee (1976, 1980), it has been suggested that the source of TC information

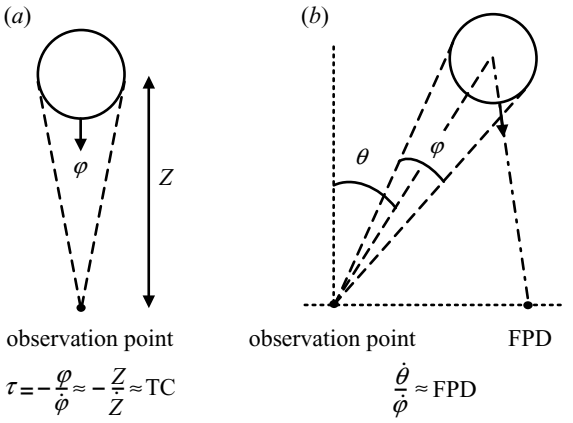

Figure 2. Two higher-order variables for objects moving on a straight trajectory with a constant velocity. (*a*) The temporal variable (τ) specifies the remaining TC for objects approaching the observation point. (*b*) The spatial variable approximates the future passing distance (FPD) in units of object size for objects that will pass the observation point.

used to time interceptive actions is a visual quantity called τ. If an object is moving with a constant velocity on a linear trajectory toward an observation point, the TC with the observation point is specified by τ, defined as the inverse of the relative rate of expansion of the optical contour of the object at the observation point (see figure 2*a*). Apart from calculating τ on the basis of the object's optical contour (or image size) at the observation point, it can be calculated for any optical angle (e.g. the optical angle between object and hand or the vergence angle), yielding different sources of TC-related information. In theory, such information could be used exclusively to determine when to initiate an interceptive movement. Several studies have presented evidence that this is indeed the case (e.g. Lee *et al.* 1983; Savelsbergh *et al.* 1991), but all of these have been challenged on methodological and conceptual grounds (Wann 1996; Tresilian 1999). Other studies have presented evidence against the exclusive use of τ (e.g. Van der Kamp *et al.* 1997; Bennett *et al.* 1999), while still others have dismissed the use of τ altogether and proposed alternative forms of TC information (Smeets *et al.* 1996; Tresilian 1999; Kerzel *et al.* 2001). Thus, as it stands, the evidence for the use of τ, regardless of its precise form, is slim at best. However, the evidence for the use of TC information in the timing of interceptive actions is very strong, even though it is unclear in what form this information is perceived. Rushton & Wann (1999) derived a model for TC estimation based on weighted combinations of optical size and binocular disparity, two cues that are both functions of the distance between the approaching object and the observer. The model is sensitive to the relative effectiveness of the two cues in estimating TC and implicitly switches its response to the cue that specifies the earliest arrival and away from the cue that is lost or below threshold.

Apart from higher-order information regarding TC, catchers and hitters may also use higher-order spatial information. Bootsma & Peper (1992) and Regan & Kaushal (1994) derived a higher-order variable specifying the distance at which an approaching object will pass the observation point in units of object size, provided that the object

moves along a straight trajectory at a constant velocity. This variable is formalized as the ratio between the rate of change of the angle between the object and the line perpendicular to the observer's frontoparallel plane and the expansion rate (see figure 2*b*). Just as for τ, evidence corroborating (Jacobs & Michaels 2003) as well as refuting (Peper *et al.* 1994; Montagne *et al.* 1999) the use of this kind of predictive spatial information has been reported. Therefore, as to the use of this kind of information, the verdict is still out. However, as noted above, it is evident from the movement reversals in the experiment of Montagne *et al.* (1999) that, if humans use this kind of predictive spatial information, it is inaccurate at movement initiation. To salvage the use of this kind of predictive spatial information, one either has to assume that the quality of the prediction improves as the action evolves in time or that the assumptions underlying its derivation were violated.

In summary, despite many effects correlated with variations in higher-order variables, no firm evidence exists that such higher-order variables are actually used in the control of interceptive actions. Data indicate that some form of TC or expansion-related information is used, but this information need not be, and probably is not, carried in τ. Similarly, it is not unlikely that some form of predictive spatial information is used, but this need not be the quantity proposed by Bootsma & Peper (1992).

3. MODELLING THE CONTROL OF INTERCEPTIVE ACTIONS ALONG THE SHORT ROUTE

'Short-route' dynamical models for the control of interceptive actions go beyond the mere identification of the informational basis of action in attempting to elucidate how perceptual quantities are coupled into the dynamics of action. This approach has been advocated as the unification of two different perspectives on perception–action coupling, namely the information-theoretical perspective of ecological psychology with its emphasis on higher-order invariants (such as τ) specifying relevant properties of the animal–environment system (such as TC) and control-theoretic (i.e. cybernetic) accounts of information-based structures supporting action (cf. Schöner 1994) (although, in our definition of short-route models, it is not critical whether the perceptual variables appear as lower- or as higher-order variables).

The first step in constructing short-route models consists of defining the perceptual and motor variables over which the control law is to be written. Therefore, the insights obtained in studies aimed at uncovering the informational basis of interceptive control often serve as basic input for short-route models. The subsequent identification of a control law consists of stipulating and modelling how the selected perceptual variables dynamically map onto motor variables, which usually take the form of state variables of the end-effector (Warren 1988). The models may be viewed as 'formal analogies' of observed behavioural phenomena, and interpreted as attempts to capture key dynamical signatures of perceptually guided actions. Such signatures may in turn be seen as the properties of neurally supported behavioural modules, which are functionally defined through their dynamics (Schöner 1994). Besides providing insights into the functional, dynamical properties of characteristic behaviours and their perceptual support, short-route models can generate testable quantitative predictions regarding these behaviours. By simulating the dynamics of short-route models it is possible to examine whether particular sources of perceptual information (e.g. τ) adequately constrain the action of interest.

Despite these merits, short-route models suffer from several shortcomings. The notion of 'formal analogy' implicitly emphasizes qualitative correspondence of dynamical features over precise quantitative matching, thus lending the mathematically agile scientist considerable liberties in formulating another 'formal analogy' if required by the data. Given the number of possible control laws (and informational variables) the number of viable 'formal analogies' for a given behavioural phenomenon is likely to be rather large. This raises the question of how one should differentiate between different models yielding similar behaviours and stability properties in particular parameter ranges.

Perhaps more important is the question of what new insights into the control of action are gained by such a differentiation. In many instances the contribution of short-route models is rather modest, as their construction is constrained solely by the behavioural phenomena of interest, perhaps in combination with some pragmatic mathematical considerations. Thus, the construction of short-route models may easily lead to the inclusion of arbitrary parameters and terms to capture aspects of local datasets such as the kinematic and stability-related features of particular behaviours. For instance, Zaal *et al.* (1999) derived a limit cycle model with several arbitrary terms to reproduce reaching trajectories to stationary and moving targets, whereas de Lussanet *et al.* (2002*a*) proposed a linear mass–spring model with a damping term defined with respect to the velocity of the equilibrium point rather than the environment, as is conventionally done, to 'account for' trajectory formation in fast-goal-directed movements. In both cases, the introduced terms seem to serve no other purpose than to satisfy the constraints that follow from the modelling goal to reproduce the observed kinematics.

Although short-route models may provide insight into, and contain intriguing hypotheses about, the stability features of perception–action patterns, it may be questioned whether the stability features of perception–action patterns may always be viewed as reflections of neurally supported behavioural modules, as suggested by Schöner (1994). Strictly speaking, short-route models preclude an understanding of the origin of stability-related features in terms of the dynamics of the subsystems (sensory, neural, biomechanical). Considering that the stabilizing properties of the musculoskeletal system may contribute significantly to the stability properties of coordinated actions (e.g. Van Soest *et al.* 1994; Van Soest & Beek 1996), it may in fact lead to erroneous conclusions when the stability properties of a particular perception–action pattern are viewed *solely* as reflections of neural control modules.

Short-route models for the control of interceptive actions may be especially useful at initial or intermediate stages of modelling when they formalize a plausible, generic control structure. An example of such a model is the RV model proposed by Peper *et al.* (1994). Peper *et al.*

closely analysed the movement trajectories of the hand (along a single lateral dimension) while intercepting balls travelling along different flight paths in relation to the time-varying position of the ball and the remaining TC (as specified by τ). Evidence was found for continuous, prospective control of the velocity of the hand. Specifically, it appeared that, during the last 400 ms or so before interception, a simple control law was obeyed according to which the momentary velocity of the hand closely matched the required hand velocity (i.e. RV) as defined by the momentary lateral distance between hand and ball divided by the remaining TC. By obeying this control law, that is, by moving the hand at the currently (and thus continuously changing) RV, the lateral hand–ball distance is reduced to zero in the remaining TC, ensuring interception of the ball without ever predicting the location of the interception point. The prospective control law identified by Peper *et al.* (1994) was supported by the movement reversals observed in the experimental study of Montagne *et al.* (1999) referred to earlier. However, in a recent experimental study very similar to the one of Peper *et al.* (1994), Jacobs & Michaels (2003) have challenged the use of lateral ball position information in favour of the predictive place-of-contact information discussed in § 2 (even though Peper *et al.* (1994) set out to examine the use of this very quantity and demonstrated that predictions of the future interception point did not conform with this information). However this issue resolves, the control law identified by Peper *et al.* shows that useful and viable insights into the control of interceptive actions can be obtained through short-route modelling efforts.

Recently, we (Dessing *et al.* 2002) further analysed the generic RV control structure inherent in two prospective controllers of hand movements in catching, both based on RV control, namely Peper *et al.*'s (1994) model and an alternative version of this model formulated by Bootsma *et al.* (1997). On the basis of a comparison with the experimental data reported in Montagne *et al.* (1999, 2000), it turned out that both models predicted overshoots of the future interception point in some conditions where no overshoots occurred in the data. Furthermore, the velocity profiles generated by the two models matched the actually observed velocity only roughly. Thus, to accomplish a better fit with the data, the proposed models need to be modified. However, owing to the nature of short-route models this would involve arbitrary extensions of the existing model constructs by adding dynamical components aimed solely at establishing a better correspondence between the output of the models and the observed kinematics. In recognition of this problem, we adopted another, more encompassing, approach that we will explain and elaborate in the sections to come.

4. MODELLING THE CONTROL OF INTERCEPTIVE ACTIONS ALONG THE LONG ROUTE

As discussed in § 3, short-route models may provide useful insights into the control of interceptive actions, but run the risk of becoming purely mathematical exercises. Furthermore, short-route models are inherently limited in that they cannot provide insights into the processes involved in the instatement of particular behaviours and their dynamic signatures. Long-route models may provide such insights by taking both behavioural and structural (i.e. anatomical, neurophysiological and biomechanical) data into account. By doing so, the arbitrariness that plagues short-route models can be reduced.

In principle, two options are available for modelling along the long route. One option is to construct dynamical models of adaptive neural networks for the processing of sensory information and the generation of task-specific motor outflow commands which are fed into a dynamical model of the musculoskeletal system. This approach, called NNDM (cf. Bullock 1998), is the one developed over the years by Bullock & Grossberg (1988, 1991). It has provided a coherent account for numerous behavioural and neurophysiological properties of relatively slow human reaching movements (Bullock & Grossberg 1988; Bullock & Contreras-Vidal 1993; Contreras-Vidal *et al.* 1997; Bullock *et al.* 1998, 1999; see also Schweighofer *et al.* 1998*b*; Spoelstra *et al.* 2000). The second option is to start off with a feed-forward model of the musculoskeletal system, involving realistic activation dynamics and force–length and force–velocity dynamics of muscles, and to identify an optimal neural stimulation of this model for performing a particular task by means of optimization. This optimal stimulation will result in movement trajectories for which the musculoskeletal dynamics are exploited to the fullest, as has been demonstrated in the study of explosive multijoint movements such as vertical jumping (e.g. Van Soest *et al.* 1994) and kicking a soccer ball (Van Soest & Beek 1996). The choice of explosive tasks is rather critical for the application of this approach for two reasons. First, such tasks may be treated as 'ballistic' in the sense that they are so fast that the role of sensory feedback (which would complicate the identification of an optimal stimulation pattern) may be conveniently ignored. Second, for explosive tasks it is relatively straightforward to formulate useful optimization criteria, such as maximal vertical velocity of the model's centre of gravity at the moment of release in the vertical jump and maximal ball velocity in the soccer kick.

Although the two modelling options may complement each other and are worthwhile to pursue in parallel, the dynamical optimization approach suffers from the problem that the identified optimal stimulation patterns take the form of fixed time-series of muscle stimulations, reminiscent of the old notion of a motor programme: 'a set of muscle commands that are structured before the movement sequence begins, and that allows the sequence to be carried out uninfluenced by peripheral feedback' (Keele 1968, p. 387). In reality, of course, the brain generates muscle commands in real-time; the optimization procedure does not address how this is accomplished. Considering that the dynamics of such generative neural processes have to be understood to come to terms with how the nervous system supports movement, and considering the evidence in favour of continuous control in the performance of interceptive actions, rapid and slow, we have chosen NNDM rather than dynamical optimization as our entry point in modelling the control of interceptive actions along the long route.

As an introduction to our long-route modelling, we first discuss Bullock & Grossberg's (1988) VITE model for trajectory formation. The VITE model (see figure 3) is a central pattern generator for voluntary movements. It

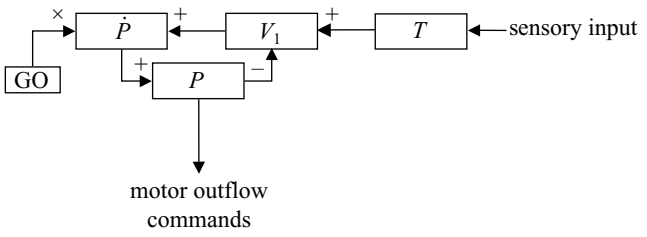

Figure 3. The VITE circuit generates motor outflow commands on the basis of sensory input. V_1 is the difference vector between the target position vector (T) and the present position vector (P). The desired velocity vector ($\dot{P}$) is determined by multiplying the V_1 with an autonomous GO signal, which can be used to scale overall movement velocity or shut off movement. P is generated internally by integrating $\dot{P}$ continuously.

contains two 'seemingly unavoidable' (Bullock 1998) types of signals: a movement vector specifying the residual required movement, and a gating signal representing a voluntary motor drive (to alter overall movement velocity or shut off movements instantaneously). The movement or difference vector (V_1) codes the difference between the target position vector (T) and the present position vector (P), which correspond to the spatial locations of target and end-effector, respectively. The multiplicative gating of V_1 by means of a so-called GO signal ($G = G_0 g$) occurs within an internal negative feedback loop and culminates in the desired velocity vector ($\dot{P}$). $\dot{P}$ is integrated continuously to determine P, which represents the model's motor outflow command. By using the internally generated P (rather than the perceived position) to determine V_1, the VITE model operates as a feed-forward controller. However, it may use proprioceptive feedback if possible or necessary (Bullock *et al.* 1998; see below). The following differential equations formally describe the VITE model:

$$\dot{V}_1 = \gamma(-V_1 + T - P), \tag{4.1}$$

$$\dot{P} = G_0 g [V_1]^+, \tag{4.2}$$

$$\dot{g}' = -Ag' + (B - g'), \tag{4.3}$$

$$\dot{g} = -Ag + g'(B - g). \tag{4.4}$$

Here, γ and A are integration rate scalars and G_0 and B are scalars. The symbol $[\arg]^+$ means max(0, arg), which stops the integration when V_1 equals zero.

Our modelling of the neural subsystem is based on the VITE model, which outputs desired kinematics. We make the auxiliary assumption that actual and desired kinematics in general diverge very little, that is, inverse dynamics control is provided by other neural systems, such as the spinal cord (e.g. Bullock & Contreras-Vidal 1993; see also Bizzi *et al.* 1982; Feldman 1986; Latash 1993) and the cerebellum (e.g. Bullock 1998; Contreras-Vidal *et al.* 1997; Schweighofer *et al.* 1998*a*,*b*; Spoelstra *et al.* 2000). For a relatively slow catching task this assumption is warranted by extensive modelling studies on inverse dynamics operations in other neural subsystems. We mention three lines of modelling. First, Bullock & Grossberg's (1989) spinal FLETE model in essence operates to linearize the peripheral motor system's response to kinematic motor outflow commands (see § 4b for a more elaborate description of the model). Second, Contreras-Vidal *et al.* (1997) modelled an adaptive cerebellar side-loop from the motor cortex to the interposed nuclei via the magnocellular zone of the red nucleus to the spinal cord. They showed how this projection might influence α-motor neuron firing in a context-dependent manner and how the cerebellum might assist in the formation of muscle synergies at the spinal level to generate the torque-time patterns needed to realize the desired kinematics. Third, Bullock *et al.* (1998) extended the VITE model to provide an account for load-sensitive and load-insensitive directional tuning in the cortical areas four and five (e.g. Georgopoulos *et al.* 1982; Kalaska *et al.* 1989, 1990; Lacquaniti *et al.* 1995). In the model the present position vector is separated into a perceived position vector (in area five) and an outflow position vector (in area four). The perceived position vector is determined by an efference copy from the outflow position vector and by Ia-afferent feedback. The outflow commands to α-motor neurons incorporate compensation for inertial and static loads, based on II and Ia afferent signals, respectively. As such, the outflow command does not only represent the desired kinematics, but also compensates for dynamic aspects of the reaching movement. These three lines of modelling provide enough support for taking behavioural data as a direct reference for the model output (i.e. desired kinematics).

In the modelling studies discussed above the main focus has been on the neural subsystem. The sensory and musculoskeletal subsystems have not been addressed in as much detail; until the study of Dessing *et al.* (2002) only movements towards stationary targets were considered, and muscle dynamics have largely been ignored or considered as something to be compensated for. In §§ 4a and 4b we will discuss our views on how to provide an account for the control of interceptive actions in which the relevant environmental information is dynamic (i.e. moving target), and how to integrate VITE-like neural networks with a more detailed dynamical musculoskeletal model.

(a) *The relative and required velocity integration to endpoint model*

In this section we summarize an extension of the VITE model that we developed to account for some basic properties of catching movements (for a full account see Dessing *et al.* (2002)). The original VITE model uses only (visual) information about object location for the planning of a hand trajectory. It contains no mechanism for the perceptual control of movement time (Beek & Bootsma 1991) and, thus, cannot explain how adequate timing is achieved in catching.

In extending the VITE model we focused on the online modulation of movement on the basis of time-related information. As became apparent in § 2, there is no consensus about the precise form of this information, although ample behavioural evidence exists for the use of TC or expansion-related information (e.g. Lee *et al.* 1983; Savelsbergh *et al.* 1991; Rushton & Wann 1999; Michaels *et al.* 2001). This behavioural evidence is matched by considerable neurophysiological support: neurons in the nucleus rotundus in pigeons (equivalent to the pulvinar nucleus in primates), the lobula giant motion detector in locusts and the cortical areas MSTd and MTd (i.e. the

dorsal parts of the medial superior temporal area and the middle temporal area) of *Macaca* monkeys all have been reported to fire in response to TC and expansion-related information (Tanaka & Saito 1989; Wang & Frost 1992; Hatsopoulos *et al.* 1995; Sun & Frost 1998; Gabbiani *et al.* 1999; Rind & Simmons 1999). Projections from the pulvinar nucleus reach the cortex (e.g. area four) via the basal ganglia and the ventral thalamus (e.g. Frost *et al.* 1990; Butler & Hodos 1996). In the VITE model the globus pallidus of the basal ganglia is the proposed site for the generation of the GO signal (Bullock & Grossberg 1991; cf. Horak & Anderson 1984*a*,*b*). We therefore postulated a TC-based modulation of the GO signal. Given the state of affairs in research on TC information, we refrained from making any assumptions about its nature: in the simulations TC was used, but τ or expansion rate would have yielded similar results for the tasks we considered. Thus, a $(\mathrm{TC})^{-1}$ signalling stage (representing neurons signalling imminency of contact) was added to the VITE model, modulating the GO signal multiplicatively. Because such a VITE model is similar to the RV model (Peper *et al.* 1994), we called it the RVITE model. The RVITE model is defined by changing equation (4.2) to

$$\dot{P} = \frac{G_0 g}{\mathrm{TC}} V_1. \tag{4.5}$$

Here, TC represents the TC of the object with the hand movement axis. The rectification of V_1 was omitted to allow for a change in movement direction. In the VITE model, movement time scales inversely with G_0. G_0 was therefore also made responsive to TC at the moment of initiation ($\mathrm{TC}_{\mathrm{ini}}$), by letting

$$G_0 = \lambda / \mathrm{TC}_{\mathrm{ini}}. \tag{4.6}$$

Here, λ is a scalar, variations of which allow for voluntary control of movement velocity.

The RVITE model prospectively brings the hand to the right place at the right time. However, as stated in § 3 the simulated kinematics of the RV model agreed qualitatively, but not quantitatively, with the observed behaviour (see figure 4). Therefore, it needed to be extended.

For the extension of the RVITE model we focused on the conditions in which the performance of the model was worst (see dotted lines in figure 4*b*). In these conditions P overshot and subsequently moved back to the interception point, whereas Montagne *et al.*'s (1999) subjects reached the interception point before interception and subsequently stayed there. This discrepancy can be explained by the fact that the RVITE model ignores the current hand and ball velocities: the current ball location only acts as a continuously changing point attractor in the spatial domain. However, when the interception point is located between the initial ball and hand position (i.e. when the hand has to move in the direction opposite to that of the ball's motion) this causes a considerable overestimation of the required hand velocity, leading to the predicted overshoots. Indeed, in such conditions systematic quantitative discrepancies occurred between data and model (see figure 4*b*), suggesting that people take both ball and hand velocity into account in coordinating the catch. The question, of course, is how. One option is that T is not specified by the current ball position, but by some prediction of the interception point. This prediction may either be

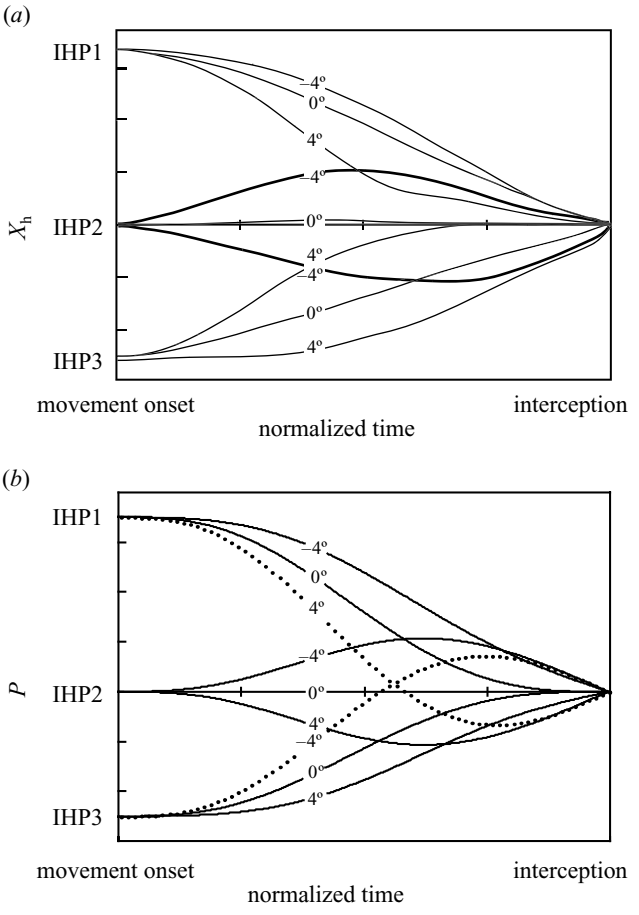

Figure 4. (*a*) Data from Montagne *et al.*'s (1999) experiment: hand position (X_h) plotted as a function of normalized movement time. IHP1–3 represent the different initial hand positions. Ball approach angles (−4°, 0°, 4°) are indicated. (Adapted from Montagne *et al.* (1999, p. 91), with permission from Springer.) (*b*) Simulated kinematics (P) of the RVITE model for the same task. Dotted lines indicate the conditions in which the RVITE model predicted overshoots that were absent in the data. Parameter values: $\gamma = 150$, $A = 1$, $B = 6$, $\lambda = 0.98$.

based on a combination of ball position and velocity (cf. Smeets & Brenner 1995) or on some higher-order variable (cf. Bootsma & Peper 1992; Regan & Kaushal 1994; Jacobs & Michaels 2003). However, as argued before, the occurrence of movement reversals implies that the initial prediction of the interception point, if any is used, must be inaccurate. Therefore, we decided to refrain from postulating exotic variables, and to follow an alternative route by postulating that the instantaneous difference between ball and hand velocity dynamically influences hand velocity (Dessing *et al.* 2002). Figure 5 suggested that, compared with the RVITE model, hand velocity should decrease when hand and ball move towards each other (in order to reduce the overshoot). Conversely, it should increase when hand and ball move away from each other, that is, when control on the basis of current position results in underestimation of the required hand velocity.

How can this principle be incorporated into the RVITE model? Neurophysiological evidence suggests that for the oculomotor system parallel parieto-frontal networks exist for both saccade control (position servo) and smooth pursuit control (velocity servo) (Tian & Lynch 1996). The

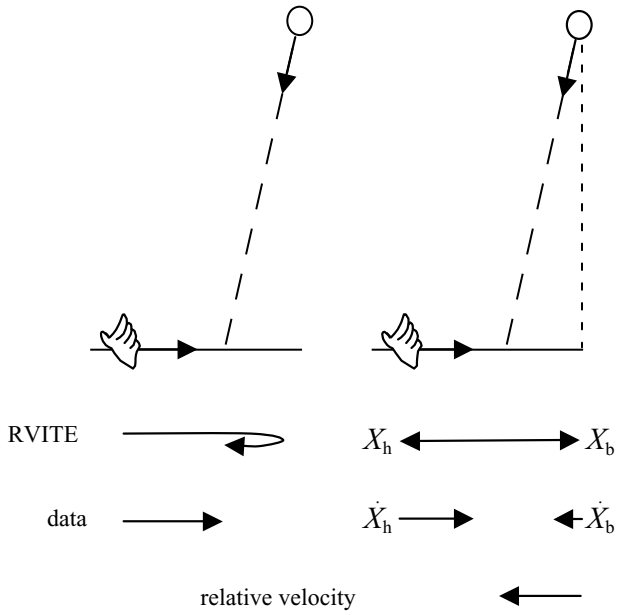

Figure 5. The left diagram indicates that the RVITE model predicts an overshoot and a subsequent movement reversal in a condition where the data do not. This is caused by the fact that the RVITE model only takes the lateral relative positions into account (i.e. X_b and X_h), as is indicated on the right diagram. When ball and hand are moving towards each other they are (through their velocities, $\dot{X}_b$ and $\dot{X}_h$) already zeroing the position difference. In this situation the RVITE model thus overestimates the current need for hand movement, resulting in an overshoot of the interception point. Taking the lateral relative velocity between hand and ball into account can decrease or eliminate these overshoots.

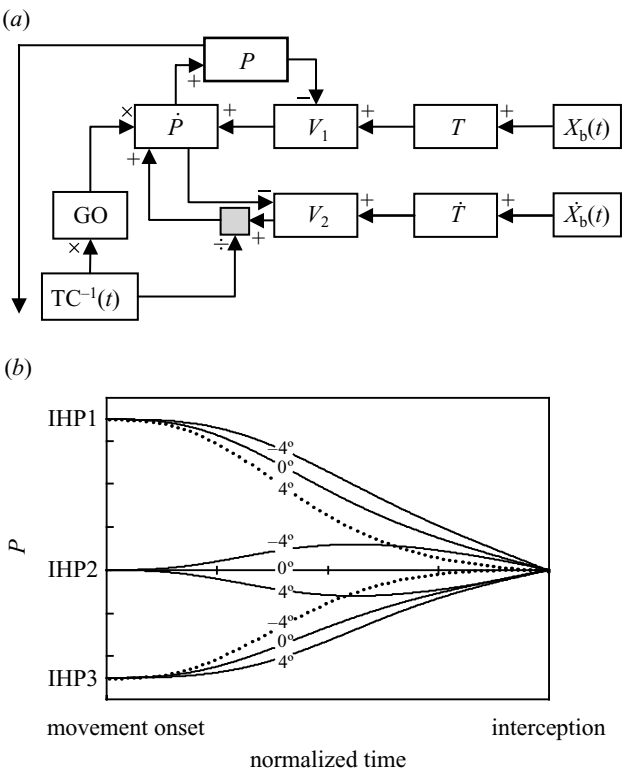

Figure 6. (*a*) In the RRVITE model V_1 and V_2 are gated by the same GO signal at the $\dot{P}$ stage. The $TC^{-1}(t)$ signal projects to the GO signal and to the V_2 output. T and $\dot{T}$ receive information about lateral ball position ($X_b(t)$) and velocity ($\dot{X}_b(t)$). (*b*) Simulated kinematics of the RRVITE model generated for Montagne *et al.*'s (1999) task. The dotted lines indicate that the V_2 prevents the overshoots and subsequent movement reversals from occurring. Parameters are the same as for RVITE, but with $\rho = 0.8$ and $\chi = 0.79$.

outputs of these networks converge at the reticular formation, a premotor centre of the oculomotor system (Yan *et al.* 2001). Considering that cross-links between oculomotor and hand movement control systems have been demonstrated in psychophysical experiments (e.g. Lazzari *et al.* 1997; Vercher *et al.* 1997), it is likely that a similar parieto-frontal parallelism exists for the control of hand movements. Therefore, a relative velocity vector (V_2) was added to the RVITE model, which codes the difference between hand and target velocity (i.e. $\dot{P}$ and $\dot{T}$). Its parallel channel projects back to $\dot{P}$ after multiplication with TC for achieving unitary consistency: $\dot{P}$ receives position-based inputs, of which the V_2 channel provides a predictive 'error' correction. We conjectured that V_2 is calculated in area five (or seven). Figure 6*a* shows the structure of the resulting RRVITE model. V_2 is specified by

$$\dot{V}_2 = \rho(-V_2 + \dot{T} - \dot{P}). \tag{4.7}$$

Here, ρ is an integration rate scalar. Furthermore, equation (4.5) was changed to

$$\dot{P} = G(V_1 + \chi \mathrm{TC} V_2), \tag{4.8}$$

where χ scales the influence of V_2 on movement velocity. Figure 6*b* shows that V_2 indeed eliminates the occurrence of erroneous overshoots in the model.

Besides the parallel nature discussed above, several lines of neuroanatomical support exist for the TC paths of the RRVITE model (Dessing *et al.* 2002; see figure 7). The LP-PUL project directly to cortical areas five and seven (Mesulam 1983; Brooks 1986; Fabre-Thorpe *et al.* 1986; Acuna *et al.* 1990; Schmahmann & Pandya 1990). This provides a basis for the proposed TC modulation of V_2 in area five (or seven). More recently, Pare & Smith (1996) provided evidence for the existence of a branched projection from the deep layers of cortical areas five and seven to the LP-PUL and to the striatum in the cat (see also Butler & Hodos 1996; Marin *et al.* 1998). The LP-PUL also project directly to the striatal areas receiving strong projections from areas five and seven (Butler & Hodos 1996; Marin *et al.* 1998). Thus, two pathways exist from the thalamic LP-PUL nuclei to the striatum: the indirect thalamo-cortico-striatal and the much more ancient direct thalamo-striatal projection. In birds and mammals, the interposed cortical processing stage has become more dominant during evolution, but strong direct thalamo-striatal projections from a few thalamic nuclei, such as LP-PUL, have survived. One plausible reason for this is that in avoiding approaching objects the faster direct path to the striatum is preferred over the slower transcortical pathway. Correspondingly, in the RRVITE model the TC–GO interaction (the thalamo-striatal-pallidal projection) is more important for successful performance. Figure 7 shows these major connections between brain areas. (Note that this schema is limited to the connections that are pertinent to the proposed model; other known connections between the same brain regions are not included.) The further differentiation that exists within each brain region

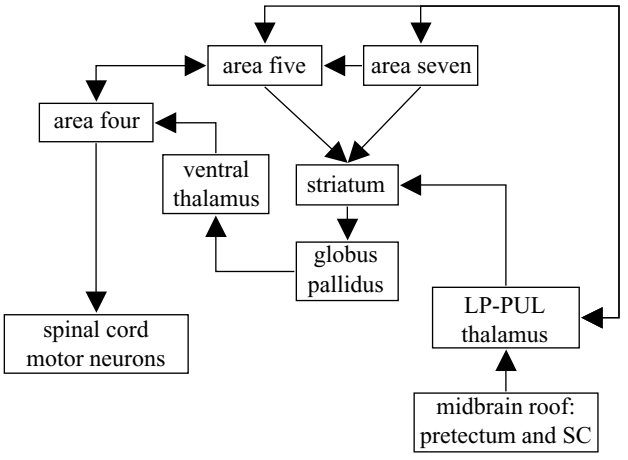

Figure 7. Known neuroanatomical connections taken as support for the RRVITE model. The projection from the LP-PUL via the striatum, globus pallidus and ventral thalamus to area four corresponds to the TC–GO–$\dot{P}$ interaction in the model. The reciprocal projections between areas four and five correspond to the $\dot{P}$–V_1 and $\dot{P}$–V_2 interactions. The projections from LP-PUL to areas five and seven correspond to the TC–V_2 interaction. SC, superior colliculus.

(local circuits involving interneurons and projection neurons, and, in some cases, multiple laminae and map-like topography) is not included in the RRVITE model. However, recent expanded treatments of local circuit details (Brown *et al.* 2000) make us confident that such details can be added without changing the dynamics emphasized in this report.

(**b**) *Integration with musculoskeletal dynamics*

The (RR)VITE model provides the spinal cord with feed-forward kinematic motor outflow commands (i.e. an intended movement). A key question is how this intended movement leads to an actual movement. As discussed in § 4, several neural subsystems have been suggested to provide the necessary inverse dynamics control. Of particular interest with regard to our VITE model extensions is the FLETE model (Bullock & Grossberg 1989, 1991; Bullock & Contreras-Vidal 1993). The FLETE model explains how the peripheral motor system (the spinal cord and musculoskeletal system) might allow separate control of joint angle and joint stiffness, respectively, based on a kinematic (VITE) control signal and a separate co-contraction signal (e.g. Humphrey & Reed 1983). Note that, besides timing and positioning, stiffness control is essential during interceptive actions as it allows adaptive tuning of dynamic end-effector properties, appropriate for the upcoming impact. The FLETE model provides an account for the operations performed by α-motor neurons, Ia- and Ib-interneurons, Renshaw cells, static and dynamic γ-motor neurons and Ia, Ib and II afferents of opponent muscles. Although the original FLETE model incorporates muscles that are modelled with quadratic force–length relationships of which the slack length depends on muscle activation, it was recently equipped with more realistic dynamic (Hill-type) muscle models (Van Heijst *et al.* 1999), of which the height rather than the zero crossing (slack length) of the force–length curve depends on muscle stimulation (e.g. Van Soest *et al.* 1994). In the resulting single-joint model the weights between the different spinal connections self-organized by means of a Hebbian-like learning rule (cf. Van Heijst *et al.* 1998). For the two-joint case Contreras-Vidal *et al.* (1997) constructed two separate FLETE models (for opponent monoarticular shoulder muscles and opponent biarticular arm muscles), which were coupled by means of a cerebellar model (to form muscle synergies) and by a feedback projection of shoulder joint receptors to elbow α-motor neurons. These couplings allowed the joint kinematics to closely follow the desired kinematics.

The modelling studies discussed above have provided many insights into the neural basis of inverse dynamics control. However, several challenges remain. A multijoint model with dynamical (Hill-type) muscles is yet to be formulated. The use of biologically realistic parameters would introduce asymmetries between opponent muscles (unlike the symmetric model used by Van Heijst *et al.* (1999)), which might threaten the separateness of angular control and stiffness control as proposed in the FLETE model. It still has to be determined to what extent all muscles in such a system can be considered as fixed opponent pairs, with minimal interconnections between their spinal modules. For instance, Contreras-Vidal *et al.* (1997) did not model any FLETE-like interaction between mono- and bi-articular shoulder muscles (e.g. monoarticular flexor and biarticular extensor), which would have been equally valid from a FLETE perspective and is also consistent with the existence of single corticospinal projections to α-motor neurons of several muscles (e.g. McKiernan *et al.* 1998; Holdefer & Miller 2002) as well as with the spinal coding of muscle synergies defined in terms of their angular equilibrium point (e.g. Bizzi *et al.* 1991; Saltiel *et al.* 2001). Future modelling should reveal the relevance of such more extensive spinal interconnections for a biologically more realistic musculoskeletal model.

The existence of kinematic planning has been questioned for explosive, high-energy movements (e.g. hitting). In particular, Van Soest & Bobbert (1998) have argued that cerebellar compensation at the spinal level discussed in § 4 would be insufficient for such tasks, because this compensation would necessarily form the predominant component of the net descending signal. For such tasks a more intimate account of neural and musculoskeletal dynamics might be required than provided thus far by NNDM. The extended VITE model with feedback and cerebellar extensions still lacks the intelligence to fully exploit the musculoskeletal dynamics; it only provides a feed-forward compensation for those effects that *can* be compensated within the constraint of the initial kinematical plan. Exploitation of the musculoskeletal dynamics may, however, be accomplished through cerebellar modulation of this kinematic plan. A possibly relevant neural projection with respect to the influence of musculoskeletal dynamics at the planning level is that from the interposed and dentate nuclei of the cerebellum to the motor cortex traversing the ventral thalamus. Through this pathway motor cortical outflow commands could be adaptively influenced (or gated), for instance by transient disinhibition of this cortical sensory-motor pathway (Bullock *et al.* 1993; Bullock 1998). This gating might allow for the selection of muscle synergies at the motor cortical level,

such that musculoskeletal dynamics are taken into account (and thus exploited) at an 'earlier' level of planning. Another way in which musculoskeletal dynamics can be exploited during explosive movements is by systematically controlling the system state before initiation: by a learned sequence of movement plans the dynamics of the propulsive release from a set-up posture can be optimized due to transient stretching of muscles and tendons (i.e. stretch–shortening cycles). This strategy is well documented for explosive movements and thus readily applies to explosive hitting tasks.

To resolve the foregoing discussion, several research questions need to be answered. First, it is necessary to study in more detail how accurately the peripheral motor system (i.e. the spinal cord in combination with the musculoskeletal system) can track an intended movement. Clearly, this requires a more extensive model of the spinal circuitry and the musculoskeletal dynamics in which realistic feedback loops are incorporated, as well as muscle-specific activation dynamics, force–length and force–velocity relations, and moment arms. We are currently involved in the development of such a model. Second, a model is required of the cerebellar projection to the motor cortex. This in effect may also require a more extensive model of cortical circuitry involved in generating motor outflow commands.

5. CONCLUDING REMARKS

In the present article we have built a case for long-route modelling in studying the control of interceptive actions. In doing so, we discussed several limitations of short-route attempts to directly model the dynamical mapping of perceptual variables onto motor variables. This critical discussion should not be interpreted as a rejection of short-route models as a means to gain insight into the control of interceptive actions. Clearly, such models may be instrumental in identifying relevant control laws that may subsequently be exploited in constructing more encompassing, long-route models. As a case in point, we highlighted the significance of the principle of RV control identified by Peper *et al.* (1994) and explained how we incorporated this principle in an explicit dynamical neural network architecture for the generation of motor control signals, the RRVITE model.

The RRVITE model has several appealing features that illustrate the merits of long-route models. First, it is not only consistent with pertinent behavioural findings, including data on the perceptual information used, but also with a large body of neuroanatomical and neurophysiological findings. In fact, it provides an integral account of these findings. It explains observed behavioural properties in terms of underlying neural connections and processes and provides, at the same time, functional interpretations for the existence of these connections and processes. As a result, the RRVITE model makes both behavioural and neural predictions, allowing this unification of knowledge to evolve further through experimentation and extended modelling. Furthermore, it contributes, together with other extensions of the original VITE model, to the development of an encompassing account of the neural control of movement to both stationary and moving objects, which stands in marked contrast with the 'stand-alone' character of many short-route models.

Obviously, singing our plea for long-route modelling does not make us blind to the possible drawbacks of this approach. Like any other more structural approach, it runs the risk of getting bogged down in incorporating too much and too detailed structural information, thereby obscuring the formative principles that are at work in instantiating particular behaviours. In addition, long-route modelling may suffer from imbalances in the degree to which the various (sensory, neural and musculoskeletal) subsystems are addressed in building larger composite models. Obviously, in the present account, which is representative for where we stand with our approach, emphasis was placed on the neural subsystem at the expense of a more elaborate treatment of the sensory and musculoskeletal system. As it stands, however, such a treatment should await further in-depth investigations into the role of the dynamical properties of these subsystems in the control of interceptive actions.

D.B. was partly supported by DARPA/ONR N00014-95-1-0409.

REFERENCES

Acuna, C., Cudeiro, J., Gonzales, F., Alonso, J. M. & Perez, R. 1990 Lateral-posterior and pulvinar reaching cells: comparison with parietal area 5a: a study in behaving *Macaca nemestrina* monkeys. *Exp. Brain Res.* **82**, 158–166.

Beek, P. J. & Bootsma, R. J. 1991 Physical and informational principles in modeling coordinated movements. *Hum. Mov. Sci.* **10**, 81–92.

Bennett, S., Van der Kamp, J., Savelsbergh, G. J. & Davids, K. 1999 Timing a one-handed catch. I. Effects of telestereoscopic viewing. *Exp. Brain Res.* **129**, 362–368.

Bizzi, E., Chapple, W. & Hogan, N. 1982 Mechanical properties of muscle: implications for motor control. *Trends Neurosci.* **5**, 395–398.

Bizzi, E., Mussa-Ivaldi, F. A. & Giszter, S. F. 1991 Computations underlying the execution of movement: a novel biological perspective. *Science* **253**, 287–291.

Bootsma, R. J. & Peper, C. E. 1992 Predictive information sources for the regulation of action with special emphasis on catching and hitting. In *Vision and motor control* (ed. L. Proteau & D. Elliott), pp. 285–314. Amsterdam: North-Holland.

Bootsma, R. J. & Van Wieringen, P. C. W. 1990 Timing an attacking forehand drive in table tennis. *J. Exp. Psychol. Hum. Percept. Perform.* **16**, 21–29.

Bootsma, R. J., Fayt, V., Zaal, F. T. J. M. & Laurent, M. 1997 On the information-based regulation of movement: what Wann (1996) may want to consider. *J. Exp. Psychol. Hum. Percept. Perform.* **23**, 1282–1289.

Brooks, V. 1986 *The neural basis of motor control*. New York: Oxford University Press.

Brouwer, A. M., Brenner, E. & Smeets, J. J. 2002 Hitting moving objects: is target speed used in guiding the hand? *Exp. Brain Res.* **143**, 198–211.

Brown, J., Bullock, D. & Grossberg, S. 2000 How laminar frontal cortex and basal ganglia circuits interact to control planned and reactive saccades. Boston University Technical Report CAS/CNS-2000-023.

Bullock, D. 1998 Neural networks research as a specialization of dynamical systems theory: learned coupling coefficients for adaptive mode switching. In *Proc. 2nd Symp. of the Institute for Fundamental and Clinical Human Movement Sciences:*

models in human movement sciences (ed. A. A. Post, J. R. Pijpers, P. Bosch & M. S. J. Boschker), pp. 69–88. Enschede, The Netherlands: PrintPartners Ipskamp.

Bullock, D. & Contreras-Vidal, J. L. 1993 How spinal networks reduce discrepancies between motor intention and motor realization. In *Variability and motor control* (ed. K. M. Newell & D. M. Corcos), pp. 183–221. Champaign, IL: Human Kinetics Press.

Bullock, D. & Grossberg, S. 1988 Neural dynamics of planned arm movements: emergent invariants and speed-accuracy properties during trajectory formation. *Psychol. Rev.* **95**, 49–90.

Bullock, D. & Grossberg, S. 1989 VITE and FLETE: neural modules for trajectory formation and postural control. In *Volitional action* (ed. W. A. Hershberger), pp. 253–298. Amsterdam: Elsevier Science.

Bullock, D. & Grossberg, S. 1991 Adaptive neural networks for control of movement trajectories invariant under speed and force rescaling: reply. *Hum. Mov. Sci.* **10**, 133–157.

Bullock, D., Contreras-Vidal, J. L. & Grossberg, S. 1993 Cerebellar learning in an opponent motor controller for adaptive load compensation and synergy formation. In *Proc. World Congress on Neural Networks*, vol. IV, pp. 481–486. Hillsdale, NJ: Erlbaum Associates.

Bullock, D., Cisek, P. & Grossberg, S. 1998 Cortical networks for control of voluntary arm movements under variable force conditions. *Cereb. Cortex* **8**, 48–62.

Bullock, D., Bongers, R. M., Lankhorst, M. & Beek, P. J. 1999 A vector-integration-to-endpoint model for performance of viapoint movements. *Neural Networks* **12**, 1–29.

Butler, A. B. & Hodos, W. 1996 *Comparative vertebrate neuroanatomy evolution and adaptation*. New York: Wiley-Liss.

Carnahan, H. & McFadyen, B. J. 1996 Visuomotor control when reaching toward and grasping moving targets. *Acta Psychol.* **92**, 17–32.

Chapman, S. 1968 Catching a baseball. *Am. J. Phys.* **36**, 868–870.

Contreras-Vidal, J. L., Grossberg, S. & Bullock, D. 1997 A neural model of cerebellar learning for arm movement control: cortico–spino–cerebellar dynamics. *Learn. Mem.* **3**, 475–502.

de Lussanet, M. H., Smeets, J. B. & Brenner, E. 2002*a* Relative damping improves linear mass-spring models of goal-directed movements. *Hum. Mov. Sci.* **21**, 85–100.

de Lussanet, M. H., Smeets, J. B. & Brenner, E. 2002*b* The relation between task history and movement strategy. *Behav. Brain Res.* **129**, 51–59.

Dessing, J. C., Bullock, D., Peper, C. E. & Beek, P. J. 2002 Prospective control of manual interceptive actions: comparative simulations of extant and new model constructs. *Neural Networks* **15**, 163–179.

Fabre-Thorpe, M., Vievard, A. & Buser, P. 1986 Role of the extra-geniculate pathway in visual guidance: effects of lesioning the pulvinar-lateral posterior thalamic complex in the cat. *Exp. Brain Res.* **62**, 596–606.

Feldman, A. G. 1986 Once more on the equilibrium-point hypothesis (lambda model) for motor control. *J. Motor Behav.* **18**, 347–353.

Frost, B. J., Wylie, D. R. & Wang, Y. C. 1990 The processing of object and self-motion in the tectofugal and accessory optic pathways of birds. *Vision Res.* **30**, 1677–1688.

Gabbiani, F., Krapp, H. G. & Laurent, G. 1999 Computation of object approach by a wide-field, motion-sensitive neuron. *J. Neurosci.* **19**, 1122–1141.

Georgopoulos, A. P., Kalaska, J. F., Caminiti, R. & Massey, J. T. 1982 On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J. Neurosci.* **2**, 1527–1537.

Hatsopoulos, N., Gabbiani, F. & Laurent, G. 1995 Elementary computation of object approach by a wide-field visual neuron. *Science* **270**, 1000–1003.

Holdefer, R. N. & Miller, L. E. 2002 Primary motor cortical neurons encode functional muscle synergies. *Exp. Brain Res.* **146**, 233–243.

Horak, F. B. & Anderson, M. E. 1984*a* Influence of globus pallidus on arm movements in monkeys. I. Effects of kainic acid-induced lesions. *J. Neurophysiol.* **52**, 290–304.

Horak, F. B. & Anderson, M. E. 1984*b* Influence of globus pallidus on arm movements in monkeys. II. Effects of stimulation. *J. Neurophysiol.* **52**, 305–322.

Hubbard, A. W. & Seng, C. N. 1954 Visual movements of batters. *Res. Q.* **25**, 42–57.

Humphrey, D. R. & Reed, D. J. 1983 Separate cortical systems for control of joint movement and joint stiffness: reciprocal activation and coactivation of antagonistic muscles. In *Motor control mechanisms in health and disease* (ed. J. E. Desmedt), pp. 347–372. New York: Raven.

Jacobs, D. M. & Michaels, C. F. 2003 The education of attention and calibration in one-handed catching. (Submitted.)

Kalaska, J. F., Cohen, D. A., Hyde, M. L. & Prud'homme, M. 1989 A comparison of movement direction-related versus load direction-related activity in primate motor cortex, using a two-dimensional reaching task. *J. Neurosci.* **9**, 2080–2102.

Kalaska, J. F., Cohen, D. A., Prud'homme, M. & Hyde, M. L. 1990 Parietal area 5 neuronal activity encodes movement kinematics, not movement dynamics. *Exp. Brain Res.* **80**, 351–364.

Keele, S. W. 1968 Movement control in skilled motor performance. *Psychol. Bull.* **70**, 387–403.

Kerzel, D., Hecht, H. & Kim, N. G. 2001 Time-to-passage judgments on circular trajectories are based on relative optical acceleration. *Percept. Psychophys.* **63**, 1153–1170.

Lacquaniti, F., Guigon, E., Bianchi, L., Ferraina, S. & Caminiti, R. 1995 Representing spatial information for limb movement: role of area 5 in the monkey. *Cereb. Cortex* **5**, 391–409.

Latash, M. L. 1993 *Control of human movement*. Champaign, IL: Human Kinetics.

Lazzari, S., Vercher, J. L. & Buizza, A. 1997 Manuo–ocular coordination in target tracking. I. A model simulating human performance. *Biol. Cybern.* 77, 257–266.

Lee, D. N. 1976 A theory of visual control of braking based on information about time-to-collision. *Perception* **5**, 437–459.

Lee, D. N. 1980 Visuo-motor coordination in space–time. In *Tutorials in motor behavior* (ed. G. E. Stelmach & J. Requin), pp. 281–285. Amsterdam: North-Holland.

Lee, D. N., Young, D. S., Reddish, P. E., Lough, S. & Clayton, T. M. 1983 Visual timing in hitting an accelerating ball. *Q. J. Exp. Psychol.* A **35**, 333–346.

McKiernan, B. J., Marcario, J. K., Hill Karrer, J. & Cheney, P. D. 1998 Corticomotoneuronal postspike effects in shoulder, elbow, wrist, digit and intrinsic hand muscles during a reach and prehension task. *J. Neurophysiol.* **83**, 1961–1980.

McLeod, P. 1987 Visual reaction time and high-speed ball games. *Perception* **16**, 49–59.

Marin, O., Smeets, W. J. & Gonzalez, A. 1998 Evolution of the basal ganglia in tetrapods: a new perspective based on recent studies in amphibians. *Trends Neurosci.* **21**, 487–494.

Mesulam, M. M. 1983 The functional anatomy and hemispheric specialization for directed attention. *Trends Neurosci.* **6**, 384–387.

Michaels, C. F. & Oudejans, R. R. D. 1992 The optics and actions of catching fly balls: zeroing out optical acceleration. *Ecol. Psychol.* **4**, 199–222.

Michaels, C. F., Zeinstra, E. B. & Oudejans, R. R. D. 2001 Information and action in punching a falling ball. *Q. J. Exp. Psychol.* A **54**, 69–93.

Montagne, G., Laurent, M., Durey, A. & Bootsma, R. 1999 Movement reversals in ball catching. *Exp. Brain Res.* **129**, 87–92.

Montagne, G., Fraisse, F., Ripoll, H. & Laurent, M. 2000 Perception–action coupling in an interceptive task: first-order time-to-contact as an input variable. *Hum. Mov. Sci.* **19**, 59–72.

Pare, D. & Smith, Y. 1996 Thalamic collaterals of corticostriatal axons: their termination field and synaptic targets in cats. *J. Comp. Neurol.* **372**, 551–567.

Pélisson, D., Prablanc, C., Goodale, M. A. & Jeannerod, M. 1986 Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Exp. Brain Res.* **62**, 303–311.

Peper, C. E., Bootsma, R. J., Mestre, D. R. & Bakker, F. C. 1994 Catching balls: how to get the hand to the right place at the right time. *J. Exp. Psychol. Hum. Percept. Perform.* **20**, 591–612.

Port, N. L., Lee, D., Dassonville, P. & Georgopoulos, A. P. 1997 Manual interception of moving targets. I. Performance and movement initiation. *Exp. Brain Res.* **116**, 406–420.

Regan, D. 1997 Visual factors in hitting and catching. *J. Sports Sci.* **15**, 533–558.

Regan, D. & Kaushal, S. 1994 Monocular discrimination of the direction of motion in-depth. *Vision Res.* **34**, 163–177.

Rind, F. C. & Simmons, P. J. 1999 Seeing what is coming: building collision-sensitive neurones. *Trends Neurosci.* **22**, 215–220.

Rosenbaum, D. A. 1975 Perception and extrapolation of velocity and acceleration. *J. Exp. Psychol. Hum. Percept. Perform.* **1**, 395–403.

Runeson, S. 1977 On the possibility of 'smart' perceptual mechanisms. *Scand. J. Psychol.* **18**, 172–179.

Rushton, S. K. & Wann, J. P. 1999 Weighted combination of size and disparity: a computational model for timing a ball catch. *Nature Neurosci.* **2**, 186–190.

Saltiel, P., Wyler-Duda, K., d'Avella, A., Tresch, M. C. & Bizzi, E. 2001 Muscle synergies encoded within the spinal cord: evidence from focal intraspinal NMDA iontophoresis in the frog. *J. Neurophysiol.* **85**, 605–619.

Savelsbergh, G. J., Whiting, H. T. & Bootsma, R. J. 1991 Grasping tau. *J. Exp. Psychol. Hum. Percept. Perform.* **17**, 315–322.

Savelsbergh, G. J., Whiting, H. T., Burden, A. M. & Bartlett, R. M. 1992 The role of predictive visual temporal information in the coordination of muscle activity in catching. *Exp. Brain Res.* **89**, 223–228.

Schmahmann, J. D. & Pandya, D. N. 1990 Anatomical investigation of projections from thalamus to posterior parietal cortex in the rhesus monkey: a WGA–HRP and fluorescent tracer study. *J. Comp. Neurol.* **295**, 299–326.

Schöner, G. 1994 Dynamic theory of action-perception patterns: the time-before-contact paradigm. *Hum. Mov. Sci.* **13**, 415–439.

Schweighofer, N., Arbib, M. A. & Kawato, M. 1998*a* Role of the cerebellum in reaching movements in humans. I. Distributed inverse dynamics control. *Eur. J. Neurosci.* **10**, 86–94.

Schweighofer, N., Spoelstra, J., Arbib, M. A. & Kawato, M. 1998*b* Role of the cerebellum in reaching movements in humans. II. A neural model of the intermediate cerebellum. *Eur. J. Neurosci.* **10**, 95–105.

Sharp, R. H. & Whiting, H. T. A. 1974 Information-processing and eye-movement behavior in a ball-catching skill. *J. Hum. Mov. Stud.* **1**, 124–131.

Smeets, J. B. & Brenner, E. 1995 Perception and action are based on the same visual information: distinction between position and velocity. *J. Exp. Psychol. Hum. Percept. Perform.* **21**, 19–31.

Smeets, J. B., Brenner, E., Trebuchet, S. & Mestre, D. R. 1996 Is judging time-to-contact based on 'tau'? *Perception* **25**, 583–590.

Spoelstra, J., Schweighofer, N. & Arbib, M. A. 2000 Cerebellar learning of accurate predictive control for fast-reaching movements. *Biol. Cybern.* **82**, 321–333.

Sun, H. J. & Frost, B. J. 1998 Computation of different optical variables of looming objects in pigeon nucleus rotundus neurons. *Nature Neurosci.* **1**, 296–303.

Tanaka, K. & Saito, H. 1989 Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *J. Neurophysiol.* **62**, 626–641.

Tian, J. R. & Lynch, J. C. 1996 Corticocortical input to the smooth and saccadic eye movement subregions of the frontal eye field in Cebus monkeys. *J. Neurophysiol.* **76**, 2754–2771.

Tresilian, J. R. 1999 Visually timed action: time-out for 'tau'? *Trends Cogn. Sci.* **3**, 301–310.

Turvey, M. T. 1977 Preliminaries to a theory of action with reference to vision. In *Perceiving, acting, and knowing: towards an ecological psychology* (ed. R. Shaw & M. Bransford), pp. 167–222. Hillsdale, NJ: Erlbaum.

Tyldesley, D. A. & Whiting, H. T. A. 1975 Operational timing. *J. Hum. Mov. Stud.* **1**, 172–177.

Van der Kamp, J., Savelsbergh, G. J. & Smeets, J. B. 1997 Multiple information sources in interceptive timing. *Hum. Mov. Sci.* **16**, 787–821.

Van Heijst, J. J., Vos, J. E. & Bullock, D. 1998 Development of a biologically inspired spinal neural network for movement control. *Neural Networks* **11**, 1305–1316.

Van Heijst, J. J., Touwen, B. C. L. & Vos, J. E. 1999 Implications of a neural network model for early sensory-motor development for the field of developmental neurology. *Early Hum. Dev.* **55**, 77–95.

Van Soest, A. J. & Beek, P. J. 1996 Perceptuo–motor coupling in the execution of fast interceptive actions. *Corpus, Psyche et Societas* **3**, 92–101.

Van Soest, A. J. & Bobbert, M. F. 1998 Towards a common language for neuro-musculo-skeletal modeling. In *Proc. 2nd Symp. of the Institute for Fundamental and Clinical Human Movement Sciences: models in human movement sciences* (ed. A. A. Post, J. R. Pijpers, P. Bosch & M. S. J. Boschker), pp. 89–91. Enschede, The Netherlands: PrintPartners Ipskamp.

Van Soest, A. J., Bobbert, M. F. & Van Ingen Schenau, G. J. 1994 A control strategy for the execution of explosive movements from varying starting positions. *J. Neurophysiol.* **71**, 1390–1402.

Vercher, J. L., Lazzari, S. & Gauthier, G. 1997 Manuo–ocular coordination in target tracking. II. Comparing the model with human behavior. *Biol. Cybern.* **77**, 267–275.

Wang, Y. & Frost, B. J. 1992 Time to collision is signalled by neurons in the nucleus rotundus of pigeons. *Nature* **356**, 236–238.

Wann, J. P. 1996 Anticipating arrival: is the tau margin a specious theory? *J. Exp. Psychol. Hum. Percept. Perform.* **22**, 1031–1048.

Warren, W. H. 1988 Action modes and laws of control for the visual guidance of action. In *Complex movement behavior: 'the' motor-action controversy* (ed. O. G. Meijer & K. Roth), pp. 339–380. Amsterdam: North-Holland, Elsevier Science Publisher B.V.

Whiting, H. T. A. 1969 *Acquiring ball skill: a psychological interpretation*. London: Bell.

Yan, Y. J., Cui, D. M. & Lynch, J. C. 2001 Overlap of saccadic

and pursuit eye movement systems in the brain stem reticular formation. *J. Neurophysiol.* **86**, 3056–3060.
Zaal, F. T. J. M., Bootsma, R. J. & Van Wieringen, P. C. W. 1999 Dynamics of reaching for stationary and moving objects: data and model. *J. Exp. Psychol. Hum. Percept. Perform.* **25**, 149–161.

GLOSSARY

FLETE: factorization of length and tension
LP-PUL: lateral posterior and pulvinar nuclei of the thalamus
NNDM: neural network dynamical modelling
RRVITE: relative and required velocity integration to endpoint
RV: required velocity
RVITE: required velocity integration to endpoint
TC: time-to-contact
VITE: vector integration to endpoint